Edgbastonia alanwillsi n. gen & n. sp. (Tateinae: Hydrobiidae s.l.: Rissooidea: Caenogastropoda); a snail from an artesian spring group in western Queensland, Australia, convergent with some Asian Amnicolidae

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Abstract

Edgbastonia alanwillsi n. gen. & n. sp. is restricted to a small group of springs on Edgbaston Station near Aramac in western Queensland where it is assumed to be relictual. It has close similarities in shell morphology to some species of Amnicolidae found in China and India and the female reproductive system has unique characters that separate it from any other described taxon attributed to the Hydrobiidae or any related family. Sequence data from COI, 16S and 18S indicate that this species is closely allied to taxa included in Jardinella Iredale & Whitley, 1938, the only genus of Hydrobiidae (sensu lato) that has been previously recognised as inhabiting the Queensland artesian discharge springs. However, several important morphological characters separate this taxon from species included in the possibly para- or polyphyletic Jardinella. Based on our molecular results, the Australasian 'hydrobiid' taxa fall within a distinct clade (Tateinae) within a broad concept of Hydrobiidae.

Key words: anatomy, Great Artesian Basin, relict, molecular phylogeny, COI, 16S, Pomatiopsidae, Amnicolidae, Edgbaston spring group

Introduction

The species described below was found in a few of the 50 artesian springs on Edgbaston Station near Aramac in western Queensland, Australia. These springs, fed by water from the Great Artesian Basin, form part of the Barcaldine Supergroup of springs (Ponder 1986, 2004; Fensham and Fairfax 2003). The springs on Edgbaston Station are also home to seven previously described endemic gastropods and an undescribed planorbid, as well as a number of other endemic invertebrates and two fishes (Ponder 2004). Most of the gastropod species confined to these springs are currently included in the genus Jardinella Iredale & Whitley, 1938, which, like many other Australasian taxa, have been treated as members of the Hydrobiidae. The use of this family name for Australasian taxa is currently under review and is used herein in the broad sense (see also Discussion).

The species that is the subject of this paper was recorded and figured by Ponder and Clark (1990) as Jardinella sp. and was known at that time from a single empty shell. Additional material found recently has, on anatomical examination, shown that this taxon is anatomically distinct from Jardinella and other ‘hydrobiid’ taxa.

Materials and methods

Material was collected by scooping sediment and vegetation using a fine mesh hand sieve in each spring at Edgbaston Station in western Queensland (for location see Fig. 1). Spring numbers follow the system used by Wager (1995).

The samples were fixed unsorted in either 95% ethanol or 10% formalin, and sorted subsequently using a dissecting microscope. Dissection was undertaken (mainly by W.-H. Z and H. F.) using a Leica MZ8 stereoscopic microscope, and drawings were done of the dissected structures using a drawing apparatus. Six females and five males were dissected.

FIGURE 1. Map of Queensland, showing location of Edgbaston Station and some towns and cities.
Shells and radulae were examined using a Leo 435 VP Scanning Electron Microscope and mounted using standard techniques.

Four specimens (one male and three females) were post-fixed in Bouin’s fixative and sectioned in paraffin with sections cut at 6 microns and stained with haematoxylin and Cason’s trichrome.

Measurements were made using a digitizing pad attached to a computer. This method and the nature of the measurements are similar to those described in detail by Ponder et al. (1989).

Molecular methods

**DNA isolation and sequencing.** DNA was isolated from individual snails with a DNeasy Blood and Tissue kit (QIAGEN) or by the method described in Wilke et al. (2006). A fragment of the COI gene was amplified with primers LCO1490 and HCO2198 (Folmer et al. 1994), LSU rRNA (16S) with primers 16Sar-L and 16Sbr-H (Palumbi et al. 1991) and SSU rRNA (18S) with the universal metazoan primers of Holland et al. (1991). For Edgbastonia, 16S and COI were amplified following the thermal cycling program of Perez et al. (2005) using 30μg Bovine Serum Albumin per PCR reaction, and with the 16Sar-L primer modified from T to A at base 11. Sequencing (in forward and reverse directions) used BigDye Version 3.1 Dye Terminator chemistry (Applied Biosystems, Foster City, CA), or used the LI-COR (Lincoln, NE) DNA sequencer Long ReadIR primer cycle sequencing kit (Amersham Pharmacia Biotech, Piscataway, NJ). Pre-existing sequences for many taxa were obtained from Genbank (see Appendix for details).

The protein-coding COI sequences were unambiguously aligned in BioEdit 7.0.4.1 (Hall 1999). The first ten base pairs (bp) behind the 3’ end of each primer were uniformly cut off, leaving a 638 bp-long overlapping fragment for the COI gene.

The alignment of the two rRNA fragments from all sources was carried out using the default settings in ClustalW (Thompson et al. 1994) resulting in fragment lengths of 514 bp and 611 bp for the 16S and 18S genes, respectively. The 16S and 18S fragments both contained two highly variable loop regions that were difficult to align (16S: positions 244–266 and 328–333; 18S: positions 146–201, 268–301). These regions were excluded from subsequent analyses. All sequences are available from GenBank (see Appendix).

Phylogenetic analysis

Phylogenetic analyses were performed on the molecular dataset using Bayesian inference (BI) as implemented in MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003). Trees were reconstructed with two parallel runs each of 2,000,000 generations, the current tree saved at intervals of ten generations and the general model suggested by Modeltest 3.6 (Posada and Crandall 1998) optimized on the fly for each data partition separately. At the end of the run, the standard deviation of split frequencies reached < 0.01 and the trees were summarized using the SUMT comment with a BURNIN value that corresponded to 25% of the samples.

Institutional abbreviations


**Results**

**Taxonomy and morphological results**

**Family Hydrobiidae sensu lato.**

As noted in the Introduction and in the Discussion, the status of this family is currently under review. Hence we refer to it as ‘Hydrobiidae’ below.

**Subfamily Tateinae Thiele, 1925**

Tateinae was introduced by Thiele (1925: 80) for the estuarine genus *Tatea* Tenison-Woods, 1879 (see Ponder et al. 1991 for a detailed description of this genus and its taxonomy) but he later (Thiele 1929) included the genus in the Hemistomiinae in Rissoidae. Iredale and McMichael (1962: 43) raised the name to family status but most authors have ignored this taxon and used Hydrobiidae without qualification. Ponder and Warén (1988) and Bouchet and Rocroi (2005) in their synopses of gastropod families use Tateinae as a subfamily of Hydrobiidae. Ioganzen and Starobogatov (1982) elevated the name to superfamly rank, a status not adopted by later authors. Synonyms of Tateinae are Potamopyrgidae F. C. Baker, 1928 and Hemistomiinae Thiele, 1929.

Although aspects of the systematics of the ‘hydrobioid’ family-group taxa remain in a state of flux, we tentatively maintain the rank of subfamily for Tateinae in a broad concept of Hydrobiidae (see also molecular results below).

The anatomy of the female reproductive system of the taxon described below is atypical of the ‘Hydrobiidae’. However, the results of the molecular analysis (see below) convincingly group it with three taxa included in *Jardinella* in Tateinae suggesting that these morphological states are derived.

**Edgbastonia Ponder, new genus**

Type species: *Edgbastonia alanwillsi* n. sp.
Etymology

Named for Edgbaston Station, near Aramac, Western Queensland. Gender feminine.

Diagnosis

Distinguished from other tateine genera by the following combination of characters: Shell ovate-conic, protoconch of about 1.1 whorls; teleocoonch with fine spiral threads, aperture with short columellar keel-like fold. Central teeth with two pairs of basal cusps, outer pair much smaller than inner. Male with narrow pallial vas deferens having several coils, penis long, simple, tapering to point, penial duct narrow throughout. Female with posterior bursa copulatrix and seminal receptacle; albumen gland shorter than capsule gland; common duct opens to large ventral chamber open to posterior capsule gland; chamber narrows anteriorly to form tube separate from anterior half of capsule gland, and extends anterior to gland.

Further details provided in species description.

Remarks

The relationships of this genus, based on our molecular results (see below), are with Jardinella s.l.. The shell is distinctive in having a columnellar fold similar to that seen in a few Australasian ‘hydrobiid’ taxa (e.g., Hemistomonia flexicolumella Ponder, 1982 from Lord Howe Island; Ponder 1982, fig. 87 and a few species of Beddomeia from Tasmania Ponder et al. 1993). A similar fold is also seen in some Asian amnicolid species, namely Erhaia (Davis et al. 1992, figs 25A, D-F, 26, 138B; Davis and Kang 1995, figs 13I–L, 23I-K) and Chencuia chinensis Liu & Zhang, 1979 (Davis et al. 1992, figs 17C,D, 18) but the fold in these taxa is much longer than in Edgbastonia, extending back about a whorl. Erhaia wufungensis (Kang, 1983) has two folds on the columella (Davis and Kang 1995, fig. 23I–K). Columnellar folds are also seen in some Asian pomatiopsids, including Wuconchona Kang, 1983 (Davis and Kang 1990, fig. 2) where the keel-like fold is located well inside the aperture so that it is not visible in apertural view, and Lacunopsis Deshayes, 1876 (Davis 1979, fig. 22e,f).

The female system differs markedly from other members of the Tateinae and also other members of ‘Hydrobiidae’ in lacking a ventral channel throughout the capsule gland. The swollen, largely separated ventral duct, which is presumably derived in large part from the ventral channel (see Discussion) apparently shares both sperm and egg transport (see also Discussion). The expanded posterior region of this duct appears to have a copulatory bursa as it contains unorientated sperm in some specimens. It opens to the capsule gland for a short distance (where it is at least analogous to a ventral channel) and, as confirmed in sections, there is no apparent additional opening to the capsule gland other than where it communicates with the albumen gland. It appears that fertilized eggs must travel down the common duct, into the expanded region at the posterior end of the capsule gland where they are moved into the albumen gland and then back into the capsule gland. Once encapsulated, the eggs then presumably move back into the expanded region and anteriorly through the separated duct (see below). If this interpretation is correct, this arrangement is unique in rissooidean gastropods.

**Edgbastonia alanwillsi** Ponder, new species.

Figures 2–9.


**Etymology**

Named for Alan Wills, owner of Edgbaston Station.

**Type material**


**Material examined**

Holotype and paratypes.


**Description**

Shell (Figs 2, 3): ovate-conic, solid, semitransparent, yellow-brown, 2.0–2.4 mm in length, 1.5–2.0 mm in width, of about 3.9–4.5 whors, narrowly umbilicate. Protoconch (Fig. 3—one uneroded specimen examined) dome-shaped, of 1.1 whors; initial portion with fine, irregular granulate microsculpture (Fig. 3C, E), edge marked by fine line (Fig. 3A, D, E, ep) followed by short section showing regular low axial folds (Fig. 3E) terminated by one or two stronger folds. Next 0.5 whor (Fig. 3A, between 1 and 2) with irregular
growth lines and similar granulate microsculpture (Fig. 3D). Both areas probably represent larval growth while encapsulated and comprise part of the larval shell. Latter section marked with clear transition to teleoconch (Fig. 3A, 2). Teleoconch with convex whorls, sutures incised, narrowly shouldered below; sculpture of irregular collabral growth lines and ridges (Figs 2D, 3B), variably developed in different specimens. Whole surface covered with very fine, closely-spaced spiral threads. Base evenly convex, axial sculpture extending across base, slightly weakening near umbilicus. Aperture ovate, slightly narrower posteriorly than anteriorly, inner lip narrowly separated from parietal wall; outer lip evenly convex, sharp, slightly thickened within. Columella narrow, with prominent fold just posterior to midpoint (Fig. 2A, B, C, E, fd) that curves around columnella for about fifth of whorl (Fig. 2C, fd); columnella, but not fold, covered with microsculpture of protruding crystals (Fig. 2E-G).

Dimensions: See Table 1.

![FIGURE 2](image)

**FIGURE 2.** Shell of *Edgbastonia alanwillsi* n. gen. & n. sp. **A, B.** Holotype (A), paratype (B). **C.** back view of shell with last part of last whorl removed to show columnellar fold (fd) and retracted operculum (op). **D.** Detail of shell sculpture on last whorl. **E.** Shell aperture tilted to show columnellar fold. **F.** Detail of columnellar fold showing full extent. **G.** Detail of microsculpture on columnella. Scales: A, B, C—0.5 mm; D, F—50 µm; E—0.2 mm; G—5 µm.

**TABLE 1.** Shell dimensions (in mm) and total whorl count. Measurements for paratypes: minimum–maximum (mean ± standard deviation).

<table>
<thead>
<tr>
<th></th>
<th>Shell length</th>
<th>Shell width</th>
<th>Aperture length</th>
<th>Aperture width</th>
<th>Length of last whorl</th>
<th>Number of whorls</th>
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<tr>
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<td>2.25</td>
<td>1.53</td>
<td>0.93</td>
<td>1.03</td>
<td>1.84</td>
<td>4.3</td>
</tr>
<tr>
<td>Figured paratype</td>
<td>2.42</td>
<td>1.72</td>
<td>0.95</td>
<td>1.08</td>
<td>2.21</td>
<td>4.5</td>
</tr>
<tr>
<td>Paratypes</td>
<td>(1.97–2.42)</td>
<td>(1.45–1.97)</td>
<td>(0.86–1.17)</td>
<td>(0.89–1.25)</td>
<td>(1.57–2.21)</td>
<td>3.85–4.50</td>
</tr>
<tr>
<td>(20, C.457754)</td>
<td>(2.15 ± 0.15)</td>
<td>(0.97 ± 0.13)</td>
<td>(0.97 ± 0.08)</td>
<td>(1.01 ± 0.09)</td>
<td>(1.78 ± 0.18)</td>
<td>(4.21 ± 0.14)</td>
</tr>
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</table>

Operculum (Fig. 4) pyriform, paucispiral, thin, flat, reddish, semi-transparent, inner side with pyriform muscle scar, otherwise simple; nucleus markedly eccentric (at about third of total length); exterior with weak growth-lines only. Retracts far into aperture (Fig. 2C, op).
Head-foot (Fig. 5A) with short, bilobed snout; cephalic tentacles of moderate length; foot apparently short (all material contracted); snout and dorsal foot (including opercular lobes) black, neck dark grey, cephalic tentacles with black to grey dorsal strip, sometimes confined to proximal half to two thirds, and around eyes, otherwise unpigmented; eyes in weak swellings at outer bases of tentacles; sole largely unpigmented, some black pigment cells visible anteriorly. Anterior third of foot partially constricted from metapodial area; propodial fold indistinct; anterior mucous gland extends across anterior edge, made up of about 20 short groups of gland cells. Sole with scattered grey to black subepithelial pigment cells. Available material contracted but sides of foot apparently lacking omniphoric groove and suprapedal fold. Mantle roof and visceral coil black, clearly visible through shell.

Mantle cavity (Fig. 5C) with well-developed ctenidium (Fig. 5C, ct) comprising 23–25 broadly-triangular filaments (n=6), apex towards right side. Osphradium (Fig. 5C, os) narrowly-oval, encircled by narrow ciliated ridge; located at middle to slightly posterior to middle of ctenidium, ctenidium 2.5–2.9 times longer. Hypobranchial gland (Fig. 5C, hg) thick, mainly located in posterior end of mantle cavity between ctenidium and rectum/pallial genital duct. Rectum “straight” (i.e., curved following right side of the pallial genital duct and, in the case of the male, the right mantle wall), anus opens well back from mantle edge (about 0.2–0.3 length of mantle cavity). Kidney and pericardium lie immediately behind posterior wall of mantle cavity. Renal opening (Fig. 5C, ro) small, simple, on middle of posterior pallial wall. Dorsal wall of renal organ with thick, densely-staining renal gland.
Digestive system: Jaws well developed, made up of multiple elements as typical for most rissoideans. Salivary glands (Fig. 6A, sg), tubular, emerge mid-dorsally from buccal mass, extend posteriorly dorsal to nerve ring and terminate just behind in some specimens, left extending further posteriorly in others. Radular sac very short, radula (Fig. 7) with central teeth: trapezoidal, basal excavation about half of tooth height; with 3–4 lateral cusps, median cusp wide, strong, sharply pointed (Fig. 7B) (blunt where wear apparent as in Fig. 7A), about twice as long as adjacent cusps; two pairs of basal cusps arise from outer side of face of tooth, close to lateral margins, their bases parallel to dorsal edge of tooth, inner basal cusps much larger than outer; basal tongue U-shaped, long, narrow, not protruding past ends of long, slightly thickened lateral edges angled at about 35° from vertical. Lateral teeth (Fig. 7E) with outer margin nearly straight, face nearly square, cutting edge just under half length of lateral wing, width of wing more than 50% of tooth-face width; with 2–3 lateral cusps on inner side, 3 on outer side, sometimes with extra denticle-like projection on outermost side of cutting edge; median cusp strong, more than twice as long as adjacent cusps, sharply pointed (Fig. 7E; blunt where wear apparent as in Fig. 7A); basal projection of lateral teeth triangular, well-developed, pointed. Inner marginal teeth (Fig. 7D) with distal half curved; narrow lateral wing on outer side of straight proximal half; cusps larger than those of outer marginal teeth; 12–16 cusps confined to outer side at the upper third, sharply pointed (Fig. 7A, or blunt when worn as in Fig. 7D). Outer marginal teeth (Fig. 7C) strongly curved, with wide flange on proximal half of outer side and moderately wide base; 19–22 small, elongate, sharp cusps on inner side of distal quarter. Anterior oesophagus with well-developed dorsal folds (Fig. 6A, df) that, in mid-oesophagus, rotate under half length of lateral wing, width of wing more than 50% of tooth-face width; with 2–3 lateral cusps on inner side, 3 on outer side, sometimes with extra denticle-like projection on outermost side of cutting edge; median cusp strong, more than twice as long as adjacent cusps, sharply pointed (Fig. 7E; blunt where wear apparent as in Fig. 7A); basal projection of lateral teeth triangular, well-developed, pointed. Inner marginal teeth (Fig. 7D) with distal half curved; narrow lateral wing on outer side of straight proximal half; cusps larger than those of outer marginal teeth; 12–16 cusps confined to outer side at the upper third, sharply pointed (Fig. 7A, or blunt when worn as in Fig. 7D). Outer marginal teeth (Fig. 7C) strongly curved, with wide flange on proximal half of outer side and moderately wide base; 19–22 small, elongate, sharp cusps on inner side of distal quarter. Anterior oesophagus with well-developed dorsal folds (Fig. 6A, df) that, in mid-oesophagus, rotate
ventrally through and behind nerve ring. Initially, ventral part of mid-oesophagus with thick lining of ciliated columnar cells (Fig. 6A, ve) which may be partly glandular (not an oesophagial gland). Thickened epithelium persists through loop of oesophagus (in contracted state) behind which cells shorten, marking beginning of posterior oesophagus. Stomach (Fig. 5B) short, weakly divided into anterior (acs) and posterior (pcs) chambers; no posterior caecum; single opening to digestive gland. Style sac (Fig. 5B, ss) slightly shorter than rest of stomach; intestine with initial vertical portion posterior to anterior end of style sac. Rectum curved along right pallial genital duct/mantle roof.

Genital system: Male: Testis (Fig. 5E) with several simple lobes emptying to few vasa efferentia (ve) joining below middle of testis as vas deferens; vas deferens forms long, coiled, narrow seminal vesicle (sv). Prostate gland (Fig. 5D) pyriform, narrow anteriorly. Pallial vas deferens narrow, with several tight coils at anterior end of prostate gland; anterior part with undulations and/or one or two small loops before entering base of penis. Penis (Fig. 5A) large, near middle of head about same distance behind eyes as between eyes; non-glandular, long and gradually tapering to simple distal point (no stylet); unpigmented apart from dorsal strip of grey in distal half. Penial duct (Figs 5A, 6B, pd) very narrow, with thin muscle layer and very narrow lumen, coiled in basal part, straightening distally.

Female: Ovary (Fig. 8C) composed of a few large lobes, with large yolky eggs. Upper oviduct opens to thick, shining, muscular inverted U-shaped oviduct (Figs 8A, 9E, ro) which continues anteriorly as S-shaped duct to anterior end of albumen gland where it joins bursal duct. Gono-pericardial duct not confirmed. Seminal receptacle (Figs 8A, B, D, 9D, sr) ovoid, with short duct, lies on left side of lower part of bursa, opens to posterior renal oviduct; contains orientated sperm. Bursa copulatrix (Figs 8A, B, D, 9D, E, b) ovoid, immediately posterior to albumen gland; epithelium tall columnar cells and unorientated sperm in lumen. Bursal duct (Figs 8A, D, 9D, E, bd) partly embedded in left side of albumen gland, moderately long, with U-shaped bend in anterior half; opens to ventro-anterior end of bursa. Common duct (oviduct proximal to junction of bursal duct; Figs 8A, B, D, 9C) narrow initially (Figs 8D, 9A), expanding before opening to capsule gland by way of short ventral slit (Figs 8D, 9B, oeg); anterior to this point, duct wider (Figs 8D, 9C) and runs along left ventral wall of capsule gland without any further connection. Expanded portion of common duct walls made up of thick layer of mainly circular muscle fibres; lumen lined with ciliated, columnar epithelium arranged in two major longitudinal ridges (Fig. 9A–C) that probably serve to separate passage of eggs and sperm. Albumen gland (Fig. 8A, B, D, ag) shorter than capsule gland, cells staining clear to pale blue, dorsal to anterior half of bursa and common oviduct. Capsule gland (Figs 8A, B, D, 9, cg) large, cells staining dense red, about half as high as long, almost entirely within pallial roof; lumen dorso-ventral slit (Fig. 9A–C, leg), simple groove ventrally except where open to common duct. Ventral muscular common duct runs anteriorly well beyond anterior end of capsule gland as free papilla-like ‘vestibule’ (Fig. 8A, B, D, v); opening small, near terminal, ventral (Fig. 8A, D, co).

FIGURE 6. Histological sections showing some details of the anterior gut and penis of *Edgbastonia alanwillsi* n. gen. & n. sp. A. Anterior oesophagus and nerve ring. B. Penis. Abbreviations: ce—cerebral ganglion; df—dorsal fold in oesophagus; p—penis; pb—base of penis; pd—penial duct; sg—salivary glands; ve—ventral epithelium of oesophagus. Scales: 100 µm.
Nervous system epiahythroid, with cerebral ganglia separated by long commissure (about third length of ganglion); optic and tentacle nerves arise from dorso-anterior ganglion, latter nerve bifurcates in tentacle; 4 labial nerves also arise from anterior part of ganglion. Supraoesophageal ganglion abuts right pleural ganglion; suboesophageal ganglion fused to left pleural, distinguished by constriction. Pedal ganglia with short commissure; no metapodial commissure. Metapodial ganglia globular, about third length of pedal ganglia. Propodial ganglia slender, difficult to distinguish from nerve. Buccal ganglia large, as wide as cerebral and about third of length. Visceral ganglion not observed. Nerve ring slightly asymmetrical with right cerebro-pedal connective slightly longer than left. Statocysts located at anterior end of pedal ganglia; with single statolith.

Remarks

The shape of the shell of the new species somewhat resembles one of the endemic ‘hydrobiids’, *Jardinella edgbastonensis* Ponder & Clark, 1990, found in the springs at Edgbaston Station. *Edgbastonia* differs in its shell being a little smaller and narrower, and having a distinctive columellar tooth. In addition, the operculum retracts only as far as the outer part of the aperture in the species currently included in *Jardinella*, whereas in *Edgbastonia* it retracts out of sight deep within the aperture (Fig. 2C), exposing the columellar tooth.

The reduced number of protoconch whorls (about 1.1—using the counting method illustrated by Hershler and Ponder 1998, fig. 17M) seen in the one suitable specimen of *Edgbastonia* (others examined being too eroded) is unusual in ‘Hydrobiidae’. The larval shell is apparently composed of two parts with the initial protoconch and a short section representing shell accretion during larval development prior to hatching, although these observations require confirmation with additional specimens.
The new species is uncommon, mostly being found in very small numbers (usually only one or a few even in samples that can contain hundreds of ‘hydrobiids’) and has been found in ten of the 50 active springs at Edgbaston Station. The type locality is only one of four springs in which more than five specimens of *Edgbastonia* have been found. Given its general similarity to one of the most abundant of the Edgbaston ‘hydrobiids’, and its rarity, it has not been observed in the field so its preferred microhabitat is unknown. It is possible that *Edgbastonia* is amphibious and, while the relatively large ctenidium, well developed hypobranchial gland and reasonably long tentacles all suggest that it is an aquatic species, these characteristics are also found in amphibious pomatiopsines (Davis 1967), along with the bipartite foot that may be present in *Edgbastonia*.

**FIGURE 8.** Female reproductive system of *Edgbastonia alanwillsi* n. gen. & n. sp. **A, B.** Female genital system from left and right sides; A, left, B, right. **C.** Ovary. **D, E.** Diagrammatic representations of female genital systems of *Edgbastonia* (D), *Jardinella* (E) and *Amnicola* (F). The arrows show the probable passage of eggs (straight arrows) and sperm (wavy arrows) through the system. Structure of E based on Hershler and Thompson (1988, fig. 8). Abbreviations: ag — albumen gland; b — bursa copulatrix; bd — bursal duct; cd — common duct; cg — capsule gland; co — common opening; o — oviduct; ocg — opening of capsule gland to common duct; oo — opening of oviduct to albumen gland; ro — renal oviduct; sd — sperm duct (‘spermathecal duct’); sr — seminal receptacle; v — vestibule. Scales: 250 µm.
FIGURE 9. Histological sections of the female genital system of *Edgbastonia alanwillsi* n. gen. & n. sp. A, B, C. Transverse sections of the pallial oviduct through the capsule gland; A, posterior part; B, about posterior third; C, anterior part. D, E. Longitudinal sections of posterior female genital system showing bursa copulatrix, common duct and capsule gland. Abbreviations: b—bursa copulatrix; bd—bursal duct; cd—common duct; cg—capsule gland; dg—digestive gland; i—intestine; k—kidney; lcg—lumen of capsule gland; mc—mantle cavity; ocg—opening of capsule gland to common duct; os—oesophagus; r—rectum; ro—renal oviduct; sr—seminal receptacle; st—stomach. Scales: 100 µm.
Molecular results
The Bayesian analysis produced the tree shown in Figure 10, with a littorinid as the outgroup. The freshwater rissooideans are differentiated into several distinct clades some of which correspond to family groups (Amnicolidae + Bythinellina + Emmericiidae; Hydrobiidae sensu lato (including in our tree Cchoiliopidae); Moitessieriiidae; Pomatiopsidae). The Australasian ‘hydroboids’ (Tateinae) are sister to Cchoiliopidae (mainly Americas), while the clade representing the restricted concept of Hydrobiidae (which includes members of Hydrobiinae, as well as other putative taxa often treated as subfamilies or, in some cases, families—Pyrgulinae, Pseudamnicolinae, Isamiitae, Horatiae and NymphophyIinea) (Europe + N. America) is sister to the Tateinae + Cchoiliopidae clade. The four Queensland taxa included in the analysis form a clade with Edgbastonia rendering Jardinella paraphyletic.

Discussion

Morphological comparisons
Based on morphology, Edgbastonia does not appear to be closely related to any extant Australian taxon but the molecular results place it with Jardinella (Hydrobiidae s.l., Tateinae). In shell characters, Edgbastonia resembles several Asian amnicolids as detailed above. Apart from a species of Erhaia recorded from northern India (Davis and Rao 1997), amnicolids are unknown from Gondwanan fragments. The Indian taxon is likely derived from China where a considerable number of similar taxa are known (e.g., Davis et al. 1992).

Morphologically, Edgbastonia is certainly a member of the so called ‘hydroboid’ group of families which includes, among others, the Hydrobiidae, Amnicolidae and Pomatiopsidae. There are few clear-cut morphological differences between these three families and they are mostly focused on the female reproductive system. Molecular data does, however, separate them (e.g., Wilke et al. 2001; and molecular results presented below).

While the molecular data clearly supports a tateine relationship, the morphological data is not so clear cut. Consequently, we have broadened the discussion below to encompass remarks on some amnicolid1 and pomatiopsid taxa in relation to some of the morphological attributes of Edgbastonia. Any relationship based on shell similarity in ‘hydroboid’ taxa is tenuous at best and, given the inconclusiveness of the morphological data we rely primarily on the results from the molecular data (see also below), and we are confident in our conclusion that Edgbastonia is a derived member of Tateinae.

The configuration of the head and foot in Edgbastonia appears to be similar to that of ‘Hydrobidae’ and Amnicolidae except for the apparent subdivision of the anterior part of the foot (which needs to be confirmed in living material). If this observation is correct, it is not the plesiomorphic condition for that group of family-group taxa (‘Hydrobioidea’) and is a condition otherwise seen in the amphibious Pomatiopsinae and Truncatellidae. The aquatic triculine pomatiopsids, hydroboids and amnicolids including erhaiines, have a simple foot.

The male reproductive system is unusual in having a tightly coiled pallial vas deferens, a feature also seen in a few species of Jardinella fromQueensland artesian springs (Ponder and Clark 1990, fig. 4E) as well as a few other Tateinae. The penis of Edgbastonia is simple and resembles those of the majority of Tateinae as well as many other ‘hydroboids’.

In particular, it is the female genital system of Edgbastonia that is unique in that it has an expanded, muscular duct that opens to a short portion of the anterior region of the capsule gland and then continues as a separate, expanded, muscular, vestibule-like combined egg + sperm duct anteriorly. The pallial oviduct of Edgbastonia could be derived from a normal ‘hydroboid’ system by the ventral channel of the capsule gland closing over along most of its length.

The female system of the Asian amnicolid Erhaia (and related taxa) is generally similar in its configuration to ‘Hydrobiidae’, it differs in lacking a ventral channel and in having a narrow ‘spermathecal duct’ which lies below the capsule gland and opens anteriorly separately from the female opening (Davis et al. 1985, 1992).

It has been hypothesised that the sperm tube (‘spermathecal duct’) is derived from the closure of the sperm groove in the ventral channel and has developed independently in several rissooidean families (Ponder 1988; Hershler and Ponder 1998; Wilke et al. 2001), including Pomatiopsidae and Amnicolidae. The sperm ducts (‘spermathecal ducts’) of amnicolids and pomatiopsines differ markedly from the condition seen in Edgbastonia in being narrow and separate from the capsule gland and, if they join with the oviduct anteriorly, it is with a small vestibular region and not the capsule gland. Davis (1979) regarded the spermathecal duct as a pomatiopsine character and led to the placement of Erhaia2 in the Pomatiopsinae by Davis et al. (1985). However, while arguing for a pomatiopsine relationship, Davis et al. (1985: 69–70) also stated that the “classification is debatable because

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1. Our concept of the composition of Amnicolidae follows Wilke et al. (2000, 2001), and includes Erhaia Davis & Kuo, 1985 (and related taxa) previously placed in the Pomatiopsidae.

2. In analyses of 16S, 18S and COI sequences, Wilke et al. (2000, 2001) showed that Erhaia was a member of a clade with Amnicola Gould & Halderman, 1840 (USA) and Marstoniops van Regteren Altena, 1936 (Europe), with Bythinella Moquin-Tandon, 1855 (Europe) a likely sister to that clade. The family-group name Erhaiiuni Davis & Kuo, 1985 (=Pseudobythinellini Davis & Chen, 1992—type genus Pseudobythinella Lu & Zhang, 1979, a junior homonym of Pseudobythinella Melville, 1956—see Kabat and Hershler 1993 for discussion) is available for the Asian taxa if subdivision of the family is necessary.
phenetically, *Erhaia* closely resembles *Bythinella* and “is closely linked to the Amnicolidae”. These authors rejected a relationship of *Erhaia* with *Bythinella* and *Amnicola* largely because of the simple penis (amnicolids as then recognised had an accessory penial appendage and duct). A penial appendage with associated duct and gland is found in *Amnicola* (Hershler and Thompson 1988) and *Marstoniopsis* (e.g., Falniowski 1987) as well as *Bythinella*. While agreeing that Amnicolidae is an appropriate location for *Erhaia* and related taxa, given the penial differences, recognition of them as a separate subgroup (*Erhaiani*) may be warranted. It is worthy of note that a very similar penial configuration to that seen in *Amnicola* also occurs in Bithyniidae which is unrelated to Amnicolidae in all but the COI tree in Wilke et al. (2001). A recently described bithyniid genus, *Pseudobithynia* Gloer & Pesic, 2006, has a simple penis (Gloer and Pesic 2006).

To derive an amnicolid (Fig. 8E) or pomatiopsid female system from a common ancestor with *Edgbastonia*, the sperm tube would have to be severed from the capsule gland, for which a separate anterior opening would be needed, and the connection of the oviduct with the glandular oviduct would have to be moved a little posteriorly to the albumen gland. The probable passage of eggs and sperm in both *Jardinella, Edgbastonia* and *Amnicola* is shown in Figure 8D-F. Both are physically separated in *Amnicola* (Fig. 8F) and are functionally separated in *Jardinella* (and other ‘hydrobiids’) by folds in separating the ventral channel from the lumen of the capsule gland. A similar functional separation is achieved in *Edgbastonia* by the pair of large longitudinal ridges that effectively divide the common duct into a dorsal and ventral channel (Fig. 9B, C). These ridges are presumably the homologues of the folds of the ventral channel of ‘hydrobiids’. We hypothesize that the condition seen in *Edgbastonia* arose from an ancestral condition similar to (but presumably convergent with) that seen in some *Jardinella* species such as *J. colmani* Ponder & Clark, 1990 (Ponder and Clark 1990, fig. 5D) where the anterior vestibule is separated from the anterior part of the capsule gland. The “vestibule” in some taxa is very large (e.g., *J. corrugata* Ponder & Clark, 1990 (Ponder and Clark 1990, fig. 12C) and *J. jesswiesae* Ponder & Clark, 1990; Ponder and Clark 1990, fig. 22C) but is in fact an expanded ventral channel which remains open to the capsule gland over all but the anterior-most part (Ponder and Clark 1990, fig. 5E).

While there is currently no evidence that there are any Australasian amnicolid taxa, Climo (1977) placed two New Zealand ‘hydrobiids’ that he had originally (Climo 1974) included in *Kuschelita* Climo, 1974, in the Japanese amnicolid genus *Saganoa* Kuroda, Habe & Tamu, 1958, a decision that he argued was justified because of their similar shells, radula, operculum and penis, as well as their phreatic habit. However, it is difficult to see how this conclusion was reached as only details of the radula, opercula and head-foot of the Japanese taxa have been published (Kuroda and Habe 1958). Haase (2008) provided some details of the female genital system of *Kuschelita*, and noted the absence of a seminal receptacle, bursa copulatrix and ventral channel but did not give any details of the configuration of the lumen of the capsule gland or specifically reject the possibility of a sperm tube. Unfortunately, the three specimens available to us for sectioning [NMNZ M174041 (2), M32474 (1)] were all males. The morphology of the central tooth of the radula (Climo 1974, fig 15E) is similar to that of *Erhaia* and related taxa although there is only one basal denticle. Climo (1974) reported that the ctenidium and osphradium were lacking in *Kuschelita* which he argued was highly modified for its subterranean habitat. Haase (2008) noted that *K. mica* lacked a ctenidium but had a well developed osphradium and hypobranchial gland and this was confirmed in our sectioned males. Clearly, determination of the relationships of *Kuschelita* must await molecular data and further anatomical information.

Molecular analysis

The tree presented in Figure 10 differs from that produced by the maximum likelihood analysis of Wilke et al. (2001, fig. 3) using COI and 18S sequences. Their tree had Cochliopiidae and Amnicolidae + *Bythinella* as sister taxa and Moitessieriidae + Bithyniidae + Hydrobiidae formed a tricotomy. Australasian ‘hydrobiids’ were not included in the Wilke et al. (2001) analysis. It should be noted, however, that both in the analysis of Wilke et al. (2001) and in the present study, deeper nodes are not well supported resulting in uncertainties relative to the relationships among higher taxa within the Rissooidea. Therefore, the resolution of the ‘hydrobioid’ family-level taxa will be subject to a much more comprehensive analysis (Wilke et al. in prep.). In the meantime, the result of our analysis raises the issue of the family status of the Australasian ‘hydrobiids’ referred to Tateinae herein. One resolution would be to treat the subclade comprising the more restricted concept of Hydrobiidae, together with the subclade Tateinae + Cochliopiidae, as a very broad concept of Hydrobiidae (i.e., as a family-rank taxon), with the subclades given subfamilial rank (i.e., Tateinae and Cochliopiinae). Alternatively, on the basis of our tree, and because Cochliopiidae is now generally

1. Liu et al. (1982) included a Chinese species in the Japanese *Akiyoshia* Kuroda & Habe, 1954 (in the subgenus *Saganoa*) and this placement was tentatively maintained by Davis et al. (1992, 1994) who pointed out that the Chinese taxon at least is related to *Erhaia*. Information on the anatomy of the Japanese taxa has not yet been published so that this relationship remains untested. Wilke et al. 2000 (p. 455) noted that *Moria* Kuroda & Habe, 1958, another Japanese taxon, has a penis like that of *Bythinella* and *Amnicola* and this observation has been confirmed by one of us (HF), but details have not been published. *Moria* falls in Amnicolidae in our molecular analysis. Davis and Rao (1997) created a new genus, *Chencaia* Davis, 1997 for the Chinese *Bythinella chinensis* Liu & Zhang, 1979, a species previously included in *Erhaia* by Davis et al. (1985) and described in full by Davis et al. (1992) as *Pseudo-bythinella*. As noted above, all Erhaiine taxa were transferred to Amnicolidae on the basis of molecular evidence.
regarded as a distinct family group, Tateinae could be raised to family level. However, given the continuing confusion surrounding the familial status of these taxa, the lack of inclusion of some key taxa in our analysis, and the lack of any clear-cut distinguishing morphological synapomorphies, we prefer to adopt a conservative approach and continue to treat Tateinae as a subfamilial group within a broad concept of Hydrobiidae pending the results of the more comprehensive analysis referred to above. By adopting this approach, we are not suggesting that the rank of Cochliopidae should be affected in the meantime.

The four Queensland taxa included in the analysis form a clade with *Edgbastonia* rendering *Jardinella* paraphyletic. This result is not surprising given the considerable morphological (Ponder and Clark 1990; Ponder 1991) and molecular (Perez et al. 2005) diversity within *Jardinella*. A major re-evaluation of the genus is currently in progress.

**FIGURE 10.** Bayesian tree based on three gene fragments for representatives of selected rissooidean families. As outgroup taxon, *Littorina obtusata* (family Littorinidae) was used as the outgroup taxon. Note the secure position of *Edgbastonia alanwillsi* n. gen. & n. sp. within the subfamily Tateinae. Bayesian posterior probabilities (when ≥ 0.95) are provided below the nodes. The scale bar indicates the expected number of substitutions per site according to the model of sequence evolution applied.
General discussion

The antiquity of the various ‘hydrobioid’ taxa is still an open question. Members of Tateinae occur in Australia, New Zealand, New Guinea, New Caledonia and a few Pacific islands including Fiji (e.g., Haase et al. 2006), suggestive of an original eastern Gondwana distribution. Davis (1979, 1981) postulated that the Pomatiopsidae divided into two main groups (Pomatiopsinae and Triculiniae) about 150 mya (in the Jurassic) prior to the break-up of Gondwana, while the Amnicolidae (as formulated in Wilke et al. 2001) has members in Europe, North America and Asia.

Whether Edgbastonia is a relictual or recently highly derived taxon is a question that can only be answered with the analysis of more Australasian taxa. The existence of a relictual species in the artesian springs of the Australian Great Artesian Basin (GAB) would, however, be of no great surprise as some other examples have been documented in Crustacea (e.g., Wilson and Keable 2004) and Platyhelminthes (e.g., Sluys 1986). These taxa have been able to survive in permanent spring habitats during the onset of aridity that occurred during the late Pliocene and continued periodically through the Pleistocene. This aridity resulted in widespread extinctions of aquatic biota presumably occurred in what is now arid and semi-arid Australia, including western Queensland (e.g., DeDeckker 1986). The group of springs on Edgbaston Station in which Edgbastonia occurs has several other endemic animals and plants, including eight other gastropods (Ponder 2004) and is undoubtedly the most significant spring group in Queensland. These springs form a subgroup of springs within the Barcaldine Supergroup located in western Queensland along with a further seven spring supergroups (Fensham and Fairfax 2003). Many of the Queensland springs have become extinct or severely degraded in the last 100 years—mainly due to drawdown resulting from water extraction for pastoral and other purposes from the GAB (Ponder 1986, 2004; Fairfax and Fensham 2003; Fensham and Fairfax 2003). Currently only two of the springs on Edgbaston Station are protected by fences which were erected in an attempt to protect endemic fish (Wager 1995).

Acknowledgements

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References


Kuroda, T. & Habe, T. (1958) Troglobiontic aquatic snails from
Kuroda et Habe (Hydrobiidae: Gastropoda) with
comments on status of the subfamily Amnicolininae.
Malacological Review 21, 81–92.
Appendix.
Family assignment, locality information, and GenBank accession numbers for the taxa studied. GenBank sequences that were generated by workers not belonging to our groups are marked with asterisks (* Liu et al. 2001; ** Haase 2005; *** Williams and Reid 2004; **** Reid et al. 1996).

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<td>China, Sichuan, Chengdu, Huang Ba</td>
<td>AF253071 AF212895 AF411141</td>
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<td><em>Gammatricula chinensis</em> Davis, Liu and Chen, 1990</td>
<td>China, Zhejiang Province, Kaiwa Co, Tong Cun Town, Bai Keng Village</td>
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